Recruitment enhancement varies by taxonomic group and oyster reef habitat characteristics

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Abstract

The rapid loss of coastal and estuarine biogenic habitats has reduced the delivery of valuable ecosystem services, resulting in calls for increased habitat restoration. Yet, a lack of information on how key habitat characteristics (e.g., area, vertical relief, age) influence the ability of restored habitats to deliver these ecosystem services hinders efforts to maximize the return on restoration investments. We conducted a meta-analysis to assess the influence of reef type (natural or restored), taxa, and restored reef size, vertical relief, age, and tidal zone on the presence and magnitude of recruitment enhancement for nekton (i.e. fish and swimming crabs). Both intertidal and subtidal reefs, as well as restored and natural reefs, enhanced nekton recruitment, though there was variation among taxonomic groups with reef types. Recruitment enhancement was more common across taxa on restored (six families) than on natural (one family) reefs. Resident nekton families were more consistently enhanced than transient families. Nekton enhancement varied with a number of restored reef characteristics. Recruitment enhancement increased with greater reef size across taxa, decreased with higher vertical relief for two families, and showed maximum recruitment around a single intertidal reef age for one family, and minimum recruitment around a single subtidal reef age for three families. Understanding variation across species in response to key design elements will improve restoration success and enhance return on investment. Moving forward, we recommend studies that vary reef habitat characteristics independently and in combination to identify how variation in these characteristics interact to influence nekton recruitment enhancement by oyster reefs.

Keywords*: habitat restoration, meta-analysis, nekton, oyster reef, recruitment enhancement, reef size, reef age, design, vertical relief*

41

42

Introduction

Coastal ecosystems consist of landscapes of biogenic habitats (e.g., oyster reefs, corals, salt marshes, mangroves, and seagrasses) that provide a range of ecosystem functions. They serve as nursery and foraging grounds for fish and invertebrates (Coen et al. 1999; Beck et al. 2001; Soniat et al. 2004), regulate energy flow and nutrient fluxes (Dame et al. 1984; Piehler and Smyth 2011; Kellogg et al. 2013), stabilize shorelines and slow erosion (Meyer et al. 1997; Piazza et al. 2005), reduce storm surge water levels (Krauss et al. 2009), and enhance biological diversity (Wells 1961; Bahr and Lanier 1981; functions are reviewed in Powers and Boyer 2014). These ecosystem functions result in a host of associated services, such as enhancing economically valuable fisheries (Peterson et al. 2003, zu Ermgassen et al. 2016), protecting shorelines and infrastructure (Meyer et al. 1997; Krauss et al. 2009; Scyphers et al. 2011), enhancing water quality by removing excess nitrogen (Piehler and Smyth 2011), and providing cultural benefits such as enhancing recreational opportunities (Carlton et al. 2016; services are reviewed in Barbier et al. 2011; Martin et al. 2016). However, degradation and loss of biogenic habitats are intensifying as human populations continue to grow and exert more pressure on coastal systems, leading to reduced aerial extent and complexity of these biogenic habitats and threatening the critical ecosystem functions they provide (Alongi 2002; Waycott et al. 2009; zu Ermgassen et al. 2012, 2013). To combat these impacts and restore ecosystem functions, habitat restoration is increasingly employed as a tool (Peterson and Lipcius 2003). Although there are many examples of successful habitat restoration efforts (e.g., oysters in protected areas, Powers et al. 2009; seagrasses in Chesapeake Bay, Lefcheck et al. 2018), overall success rates for many projects, including those in coastal habitats, are moderate (Bayraktarov et al. 2016), and ecosystem functions may remain reduced in restored versus intact habitats (Rey Benayas et al.

66 2009). Understanding how particular ecosystem functions vary across a range of restored habitat
67 characteristics (e.g., areal extent, age) can inform future habitat restoration efforts by helping
68 decision-makers better predict how restoration design elements may influence service delivery.
69 Re-establishing biodiversity is a common goal of habitat restoration (Peterson and
70 Lipcius 2003; Rey Benayas et al. 2009), yet distribution patterns of fauna among patchy habitats
71 are difficult to predict because they are shaped by processes occurring at various scales of space,
72 time, and ecological organization that often differ from the scales at which patterns are observed
73 (Levin 1992). Understanding how restoration design influences faunal abundances across
74 multiple taxa will enhance the ability of restoration practitioners to increase the return on
75 investments made by future conservation and restoration efforts. Oyster reefs are broadly
76 distributed and augment populations of many faunal species (Zimmerman et al. 1989; Coen et al.
77 1999; Rodney and Paynter 2006). Although many studies have documented augmented faunal
78 abundances by oyster reefs, the degree of enhancement varies considerably among studies,
79 species, and ocean basins (e.g., Robillard et al. 2010; Kingsley-Smith et al. 2012; Nevins et al.
80 2014; synthesized in zu Ermgassen et al. 2016). This variation in recruitment enhancement could
81 stem from several differences among studies due to varying habitat characteristics, including reef
82 areal extent, vertical relief, tidal zone (e.g., subtidal vs. intertidal) tidal elevation, salinity, or
83 landscape setting (Lenihan 1999; Lenihan et al. 2001; Lehnert and Allen 2002; Grabowski et al.
84 2005), but the potential role of these factors has yet to be thoroughly examined.
85 We synthesized information from Eastern Oyster (*Crassostrea virginica*) restoration
86 studies across the U.S. to assess the potential influence of habitat characteristics incorporated
87 into reef restoration designs on the abundance of reef-associated nekton (specifically fish and
88 swimming crabs in association with oyster reefs). Augmentation of nekton can occur through

89 recruitment enhancement of early life stages (which includes improved settlement, growth, and
90 survival of juveniles; Beck et al. 2001), or enhanced growth and reproductive effort of adults
91 (e.g., by concentrating food resources and enhancing foraging and spawning opportunities;
92 Peterson et al. 2003, Powers et al. 2003) relative to unstructured habitats. Because growth
93 enhancement likely contributes far less to lifetime augmented nekton production by oyster reefs
94 than recruitment enhancement (Peterson et al. 2003, zu Ermgassen et al. 2016), our synthesis
95 focused on recruitment enhancement. We specifically examined whether reef recruitment
96 enhancement varies by taxonomic group and 1) reef type (i.e., natural or restored reefs) or 2) the
97 size, vertical relief, or age of restored reefs. Our ultimate goal was to provide information for
98 resource managers to guide future habitat restoration efforts.
99

100 **Methods**

101 ***Literature review***

102 First, we determined the variety of reef characteristics reported by studies investigating
103 nekton recruitment enhancement by oyster reefs using citations from the reference list of a
104 recently completed meta-analysis (zu Ermgassen et al. 2016). We identified nekton families that
105 were regularly reported at oyster reef and control habitats, including both resident (i.e., species
106 that feed, breed, and shelter on reefs long after initial recruitment, Coen et al. 1999; Harding and
107 Mann 2000) and transient (i.e., species that recruit to structured habitats but are more widely
108 distributed across multiple habitats after recruitment, Harding and Mann 2001) reef-associated
109 species. We also performed forward searches in Google Scholar on two published syntheses:
110 Peterson et al. (2003) and zu Ermgassen et al. (2016). We retained studies that met the following
111 criteria: 1) authors quantified density or relative abundance of target nekton families at both

oyster reefs (or experimental units that contained oyster shell and served as a mimic for reef habitat; e.g., Humphries et al. 2011) and unstructured mud or sand habitats within the same study; 2) restored reefs used oyster shell, including shell piles, cultch, bagged shell, or shell piles from other species (e.g., surf clams) if topped by oyster shell; 3) restored reefs were within the tidal extent of natural reefs (< 10 m deep relative to mean low water [MLW] at the base of the reef; Kennedy and Sanford 1999) , 4) fishing gear(s) quantitatively censused juveniles; and 5) authors reported densities or abundances of target nekton by species or family.

Data Extraction

We extracted densities or abundances, measures of spread (standard deviation or standard error), and sample sizes of each nekton species from oyster reefs and their paired unstructured control habitat patches. We extracted data for nine nekton families, including reef residents: toadfish (Batrachoididae), blennies (Blenniidae), gobies (Gobiidae), and skilletfish (Gobiesocidae, which were later removed due to limited data availability); and reef transients: grunts (Haemulidae), snappers (Lutjanidae), swimming crabs (Portunidae), drums (Sciaenidae), and porgies (Sparidae; Table 1). We normalized densities to mean individuals m^{-2}, abundances to mean individuals per sample (relative abundances), and measures of spread to one standard error of the mean (Appendix B). We extracted tidal zone (subtidal or intertidal), reef type (restored or natural), restoration method (reefs restored with or without live oysters), and when available, reef size (standardized to m^2), vertical relief (distance from bare sediment to the highest point on the reef, standardized to m), tidal elevation (at the base of the reef, in m relative to MLW), adult oyster density (individuals m^{-2} > 75 mm in shell height, or specified as adult by the authors), and the year of restored reef construction, from which we calculated reef age (Table A1; Appendix B).

135 ***Analyses***

136 To compare nekton recruitment to oyster reefs versus unstructured control habitat, we
137 calculated log response ratios (LRRs, Hedges et al. 1999) with 95% confidence intervals by
138 family (Appendix B). An LRR with CIs > 0 implies that nekton recruitment was enhanced by
139 oyster reefs, an LRR with CIs < 0 implies the opposite, and an LRR with CIs that include 0
140 implies no difference in recruitment between oyster reef and control habitats. For each research
141 question, we assessed data publication bias with funnel plots (Appendix C) and data availability
142 with mosaic and violin plots (Appendix D).

143 To assess whether recruitment enhancement varied as a function of reef type (natural or
144 restored) and nekton family, we conducted linear mixed model analyses separately for intertidal
145 and subtidal reefs that included two categorical factors (reef type and nekton family) and their
146 interaction as fixed effects, with study as a random effect. We conducted mixed model analyses
147 separately by tidal zone since subtidal and intertidal habitats harbor different nekton
148 communities (Lehnert and Allen 2002), and subtidal and intertidal oyster reefs are distributed
149 unevenly in our database: intertidal reefs are more prevalent on the Atlantic coast and subtidal
150 reefs are more common in the Gulf of Mexico (Fig. 1; Tab. A1). Furthermore, the reef
151 characteristics in our database differed across tidal zones (Fig. D1-D12). We removed any family
152 that was represented by fewer than three independent studies and/or fewer than 10 independent
153 LRRs ("NA" on Fig. 2). Results of randomization and resampling in support of these criteria are
154 presented in Appendix E.

155 To evaluate the effects of restored reef characteristics (i.e., reef size, vertical relief, and
156 age) on recruitment enhancement, we focused on restored reefs only, and performed linear mixed
157 effect regression models with orthogonal polynomials (first and second order) for the continuous

158 reef characteristics as fixed effects, and study as a random effect. We conducted separate
159 analyses for each reef characteristic, nekton family, and tidal zone. We did not model families
160 represented by fewer than three independent studies and/or 10 independent LRRs covering
161 different values of the reef characteristics (e.g., reef sizes, vertical reliefs, or ages; "insufficient
162 data" in Figs. 3-8), and results are not reported or plotted for models that did not converge.
163 Since not all families were represented at all values of each reef characteristic (e.g., all vertical
164 reliefs or sizes), we performed separate analyses for each family and included all available data
165 (but for combined-family approaches, see Appendix B for methods and Appendix E for results).
166 We also examined the influence of tidal elevation on recruitment enhancement for each family
167 using linear mixed effect regression models with orthogonal polynomials (first and second order)
168 for tidal elevation as a fixed effect and study as a random effect (Appendix E). Where models
169 indicated that predictor variables are on substantially different scales (i.e. reef size) we rescaled
170 using natural log transformation.

171 All models were weighted by sample size (Appendix B). All analyses were conducted in
172 R 3.6.1 (R Core Team, 2019) on the RStudio IDE 1.2.1335 (RStudio Team, 2019).

173

174 **Results**

175 We extracted density or relative abundance comparisons from 28 studies (Table A1) that
176 generated 1,820 LRRs across eight target nekton families (excluding skilletfish), represented by
177 51 species (Table 1). Studies were distributed along the Atlantic and Gulf of Mexico coastlines
178 from New Jersey to Texas, USA, across 25 embayments (Fig. 1). Funnel plots indicated no
179 evidence of publication bias (Fig. C1).

180 ***Restored vs. natural reefs (reef type)***

181 Recruitment enhancement on intertidal reefs varied interactively by family and reef type
182 (Fig. 2a; family * reef type, $F_{4,790} = 8.25$ $p < 0.001$). In the intertidal, recruitment was frequently
183 enhanced on restored reefs (i.e., LRR > 0 for two resident families: toadfish and blennies and
184 three transient families: grunts, snappers and porgies; Fig. 2a), but not on natural oyster reefs
185 (i.e., LRR = 0; Fig. 2a). Recruitment enhancement on subtidal reefs varied by family and was
186 marginally related to reef type, but not their interaction (Fig. 2b; family, $F_{3,513} = 8.19$, $p < 0.001$;
187 reef type, $F_{1,11} = 3.53$ $p = 0.09$; family * reef type, $F_{3,513} = 1.81$, $p = 0.15$). Five families (three
188 resident: toadfishes, blennies, and gobies; two transient: grunts and porgies) were enhanced at
189 subtidal restored reefs (Fig. 2b), and one resident family (blennies) was enhanced on subtidal
190 natural reefs (Fig. 2b). Swimming crabs were more abundant on unstructured sedimentary habitat
191 than natural reefs in both intertidal and subtidal zones (i.e., LRR < 0; Fig. 2a-b), though they did
192 not differ between restored reefs and unstructured habitat in either zone (Fig. 2a-b). In the
193 subtidal zone, drums were more abundant on unstructured sedimentary habitat than restored reefs
194 but did not differ between natural reefs and controls (Fig. 2b).

195 ***Restored reef characteristics (reef size, vertical relief, and age)***

196 Recruitment enhancement differed with reef size for only one family (blennies; Fig. 3-4).
197 On intertidal reefs, there was no relationship between blenny recruitment and reef size (natural
198 log transformed). On subtidal reefs, there was a marginal U-shaped relationship between blenny
199 recruitment enhancement and subtidal reef size ($t_{54.7} = 1.78$, $p = 0.08$), with recruitment
200 enhancement decreasing from 0.5 m^2 to 28.3 m^2 and increasing from 28.3 m^2 to 50.3 m^2 (Fig.
201 4b).

202 Recruitment enhancement of several families (grunts, drums, and blennies) varied with
203 reef vertical relief (Fig. 5-6). Drum enhancement varied with vertical relief on intertidal reefs in

204 a U-shaped pattern (Fig. 5g, $t_{6.9} = 2.66$, $p = 0.03$), though a single experiment, at a vertical relief
205 of 0.48 m with 20 independent replicates, appears to drive this relationship (Fig. 5g).
206 Enhancement of blennies on subtidal reefs tended to decrease with increasing vertical relief (Fig.
207 6b; $t_{6.6} = -1.96$, $p = 0.09$). On subtidal reefs, drum enhancement decreased as vertical relief
208 increased (Fig. 6g; $t_{7.44} = -2.52$, $p = 0.04$).
209 Recruitment enhancement of some families was also correlated with reef age (Figs. 7-8).
210 On subtidal reefs, toadfish enhancement varied with reef age in a U-shaped pattern, decreasing
211 from reefs that were between 0 and approximately 4 years of age, and then increasing from reefs
212 aged approximately 4 to 6 years ($t_{77.6} = 2.43$, $p = 0.02$; Fig. 8a). Drum enhancement responded
213 similarly to reef age on subtidal reefs ($t_{126.8} = 7.25$, $p < 0.0001$; Fig. 8g), decreasing from 0- to 4-
214 year-old reefs, then increasing on six-year-old reefs (Fig. 8g). Porgy enhancement on subtidal
215 reefs also varied similarly with reef age ($t_{56.2} = 2.56$, $p = 0.01$; Fig. 8h), decreasing on reefs
216 between 0- to 3-years old, and then increasing on six-year-old reefs (Fig. 8h). Porgy
217 enhancement on intertidal reefs tended to vary with reef age in a hump-shaped pattern (Fig. 7h,
218 $t_{17.7} = -2.04$, $p = 0.06$), with recruitment enhancement increasing from 0 to 7 years, and
219 decreasing from 7 to 13 years.
220

221 **Discussion**

222 Our analyses confirmed that both natural and restored oyster reefs enhance nekton
223 recruitment, and we further demonstrate that the magnitude of this enhancement is as strong or
224 stronger on restored reefs as natural reefs for five nekton families (Fig. 2). The magnitude of
225 enhancement also varied by family and tidal zone and key characteristics of restored reef design
226 (i.e., reef size, reef vertical relief, and reef age) also influenced recruitment enhancement of

227 fishes and swimming crabs. Nekton recruitment enhancement tended to increase with intertidal
228 reef size, though increases in vertical relief decreased enhancement, particularly at subtidal reefs.
229 Enhancement of many nekton species occurred immediately, though enhancement of porgies
230 peaked around 6 years on intertidal reefs, and enhancement of toadfish, drums and porgies was
231 lowest at intermediate ages (about 3-4 years) on subtidal reefs. Further data are needed to
232 examine whether recruitment enhancement is sustained over longer time periods.

233 Review of past restoration projects suggest that enhancement of nekton recruitment is
234 generally greater on restored than on natural reefs. The enhancement by restored reefs supports
235 earlier findings that nekton communities respond rapidly to oyster reef restoration efforts
236 (Lenihan et al.2001; Grabowski et al. 2005; La Peyre et al. 2014) and highlights the utility of reef
237 restoration as a technique to recover nekton abundances. We do not know why restored reefs
238 more consistently augmented nekton than natural reefs, but past or current exposure of natural
239 reefs to destructive harvesting practices that reduced their habitat quality may have contributed
240 to this difference. Given the dramatic losses of oyster populations to overharvesting and other
241 contributing factors (reviewed in Kirby 2004), remaining natural reefs may be degraded and
242 exhibiting reduced function (zu Ermgassen et al. 2012; 2013), whereas restored reefs are often
243 protected from harvest (e.g., Dunnigan 2015). Only 10 of 29 studies in our analysis reported
244 susceptibility to harvest, with even fewer providing specific harvest methods and amounts,
245 precluding an analysis of the effects of harvest on nekton recruitment enhancement in this study.

246 Habitat patch size can mediate the population dynamics of mobile species (Hanski 1999):
247 larger habitat patches have lower metapopulation extinction rates (MacArthur and Wilson 1967,
248 Hanski 1999) and alleviate negative edge effects in fragmented landscapes (Reis 2004). Thus, we
249 expected enhancement of fish and mobile crustacean recruitment to increase with restored reef

250 (patch) size. Our analyses of individual families were not significant but there were positive
251 trends at intertidal reefs, and our combined-family analysis provided additional support that
252 recruitment enhancement increases with intertidal reef size (Fig. E2a). For subtidal reefs, the
253 influence of reef size was taxon-dependent (Fig E2b), consistent with findings from the habitat
254 fragmentation literature (Eggleston et al. 1999; Johnson and Heck 2006). Relationships between
255 fish recruitment enhancement and reef size may be more consistent within a region than across
256 regions. For instance, the density of commercial fishes within marine reserves increased with
257 reserve size when marine reserves within a single region were compared to unprotected spaces
258 (Edgar and Barrett 1997; Claudet et al. 2008), yet Lester et al. (2009) found no relationship
259 between density enhancement and MPA size when synthesizing MPAs globally. Additionally, an
260 over-representation of small reef sizes in our analysis, as in the global analysis of MPAs (Lester
261 et al. 2009), may have hindered our ability to detect an impact of habitat size. Reefs in our
262 analysis ranged in size over four orders of magnitude (0.45 to > 8000 m^2), though greater than
263 70% of restored reefs that reported sizes were ≤ 50 m^2 (Fig. D3). Given the magnitude of
264 degradation that has occurred in many estuaries in the U.S. and elsewhere, extensive restoration
265 efforts are necessary. Studies that include larger (i.e., ~ 100 – 1000 m^2) restored reefs are needed
266 to better define the relationship between reef size and recruitment enhancement and determine
267 whether there are optimal or minimum sizes necessary to benefit target species.
268 The vertical relief of a reef can influence oyster survival (Taylor and Bushek 2008;
269 Colden et al. 2017). We expected that greater relief would also increase augmentation of fish and
270 mobile crustacean abundances, as taller reefs are less likely to be influenced by bottom-water
271 hypoxia (Lenihan et al 2001), more likely to avoid sedimentation and sustain oyster populations
272 (Taylor and Bushek 2008; Colden et al. 2017), and potentially provide greater reef complexity

and refuge quality. Recruitment enhancement of individual families did not vary consistently with vertical relief on intertidal reefs, which may be more strongly influenced by seldom-reported tidal emersion (determined by a combination of vertical relief, tidal elevation, and tidal range in the embayment; Fodrie et al. 2014; Walles et al. 2016) than vertical relief alone. On subtidal reefs, we found evidence that increasing reef vertical relief decreased recruitment enhancement of two families. Perhaps greater vertical relief on these reefs provided more accessible area to support a wider variety of predators, leading to these negative relationships. Prior studies have described thresholds in initial height of subtidal restored oyster reefs (~0.2 – 0.45 m) for the persistence of oyster growth (Lenihan 1999; Powers et al. 2009; Schulte et al. 2009; Lipcius et al. 2015; Grizzle and Ward 2016; Colden et al. 2017). Our results suggest a threshold under which nekton recruitment is enhanced (< 1 m) by greater reef height; from 0 to 1 m reef height, small gains in reef height can lead to substantial increases in nekton recruitment enhancement until they reach a maximum and then decline above around 1 m reef height. Thus, designing reefs to optimize oyster recruitment will likely influence enhancement of fish families. Although the mechanisms driving this relationship are not clear, if reefs are preferentially restored in areas that are not typically subjected to hypoxia, then reefs with higher vertical relief may not be necessary. Given that constructing high relief reefs is more expensive and requires greater amounts of shell material, restoration decision-makers could increase the aerial extent of restored reefs in areas where low-relief reefs will be effective.

Variability in recruitment enhancement across families may also be attributable to their degree of reef fidelity (e.g., reef residents vs. transients). Oyster habitat is considered an essential habitat for resident species long after initial recruitment (Coen et al. 1999; Harding and Mann 2000), whereas transient species spend less time on reefs and are more widely distributed across

296 multiple structured habitats (Harding and Mann 2001). In our database, some intriguing potential
297 differences between residents and transients emerged. Each resident species we examined
298 demonstrated recruitment enhancement, whereas only two families of transient species were
299 enhanced (grunts and porgies), and two demonstrated lower recruitment at some oyster reefs
300 (drums and crabs; Fig. 2). Drums are transient among estuarine habitats and utilize oyster reefs
301 over non-vegetated habitat in some studies (Lenihan et al. 2001; Kingsley-Smith et al. 2012),
302 though they utilize marsh edges and subtidal areas over oyster reefs in other studies (Stunz et al.
303 2010). Low or no recruitment of drums to oyster reefs may therefore reflect functional
304 redundancy of structured habitats (Grabowski et al. 2005; Geraldi et al. 2009) and/or alternative
305 habitat selection, particularly in intertidal zones where alternative structured habitats are often
306 readily available. Understanding the influence of coastal habitat landscapes, rather than just
307 individual habitats, on faunal abundance is a key research priority for informing habitat
308 restoration efforts (Gilby et al. 2018). In the case of the Blue crab, *Callinectes sapidus*, previous
309 studies found blue crab to be enhanced by oyster reef in the Gulf of Mexico, but not in the
310 Atlantic coast (zu Ermgassen et al. 2016). It is possible that by using data from both regions in
311 this analysis, this regional enhancement was masked in our results.
312 Several other factors not included in our analysis likely influence nekton recruitment
313 enhancement by oyster reefs. For instance, nekton densities on oyster reefs, including many of
314 our target families, fluctuate seasonally (Lehnert and Allen 2002; Shervette and Gelwick 2008).
315 Many studies in our synthesis reported densities pooled across repeated time points, precluding
316 an analysis of seasonality. Further, our synthesis included studies conducted across different
317 latitudes where seasonality effects may differ. Although we were not able to explicitly evaluate

318 the effects of seasonality, assuming nekton do not change their relative use of oyster vs.
319 unstructured habitats by season, this omission should not confound our results.

320 We are often forced to make assumptions about whether ecosystem services from
321 restored habitats are consistent over time because of the lack of temporal data on service delivery
322 (Barbier et al. 2011; Grabowski et al. 2012). While many studies reviewed in this meta-analysis
323 have documented that fish and invertebrate communities respond quickly to restoration efforts,
324 ecological theory predicts that recruitment enhancement will vary through time. For example, as
325 restored reefs age, we expect their associated communities will undergo succession (Connell and
326 Slatyer 1977; Manley et al. 2010; Quan et al. 2012). Recruitment was reported at intertidal
327 restored reefs 0 – 13 years old in our study. Though reef age was not a strong predictor of
328 recruitment enhancement in our analyses, porgies provided some evidence for a maximum
329 recruitment enhancement at intermediate reef ages, while recruitment enhancement data for
330 intertidal reefs aged 8 – 12 years are not available for any family and represent a data gap (Fig.
331 7). For restored reefs in the subtidal, a minimum recruitment enhancement value at reefs aged 3 –
332 4 years were represented by data from a single study that reported annual recruitment on reefs >
333 1 year old (Lenihan et al. 2001). Additional studies are needed to provide further evidence for
334 this relationship and address the data gap beyond 6 years old for subtidal reefs. Several studies
335 pooled densities across years (4 of 21 studies that reported reef construction date, Appendix A),
336 indicating that services were consistent over the time these studies were sampled (e.g., La Peyre
337 et al. 2014). However, the limited data for nekton recruitment enhancement over a decadal
338 timescale (but see Ziegler et al. 2018) challenges our ability to project whether ecosystem service
339 delivery remains constant or varies temporally at the scale of several years to decades. Thus,

long-term studies investigating the degree to which nekton enhancement varies with reef age would be particularly useful.

Reef habitat complexity (the physical structure of an environment) is predicted to increase with reef age as oysters settle atop one another and grow vertically in the water column (Bahr and Lanier 1981; Grabowski et al. 2005; Rodriguez et al. 2014; Ziegler et al. 2018). Such habitat complexity has been linked to habitat quality for associated communities, with interstitial refuges that decrease interaction strengths (i.e., predation, Humphries et al. 2011) and increase rugosity, which alters water flow and enhances larval settlement opportunities (Breitburg et al. 1995). Oyster density and biomass are often used as quantitative measures of reef complexity (Baggett et al. 2015); thus, we expected augmentation of fish and mobile crustaceans to increase with oyster density and biomass on oyster reefs, even in the absence of explicit information about reef age. However, we could not assess nekton responses to oyster density, as only five out of the 22 studies of restored reefs in our database reported oyster density, and fewer yet reported biomass.

Syntheses across restoration efforts can identify potential influences of reef characteristics on recruitment enhancement, determine restoration designs that are most beneficial to target species, and help assess tradeoffs among targeted services. Future experiments that manipulate multiple restoration design factors orthogonally will further our understanding and predictive capacity of how they potentially interact to influence ecosystem service delivery by restored habitats, including nekton recruitment enhancement at oyster reefs. Such manipulations are difficult at scales relevant for restoration, so data syntheses are also a critical tool for advancing restoration science. Future synthesis efforts will be facilitated by consistent reporting across restoration efforts; therefore, we highlight Baggett et al.'s (2015)

363 recommendations for reporting universal oyster reef metrics (project footprint and reef area, reef
364 vertical relief, oyster density, and oyster size-frequency distribution) and environmental variables
365 (water temperature, salinity, and for subtidal reefs, dissolved oxygen) from all oyster restoration
366 projects, in addition to densities of target species when reefs are intended to benefit nekton. We
367 also support Walles et al. (2016)'s recommendation to add tidal emersion for intertidal reefs to
368 this set of recommendations, and we further suggest that tidal elevation, reef age at the time of
369 sampling, and exposure to oyster harvest be reported for effective comparisons across restored
370 reefs. Given the magnitude of restoration needed to recover lost ecosystem services from
371 biogenic habitats, experimental and synthetic efforts aimed at guiding restoration decision-
372 making are critical.

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613 **Supporting Information**

614 Supporting information may be found in the online version of this article.

615 **Appendix A.** Key features and citations for studies included in the meta-analysis.

616 **Appendix B.** Detailed description of methods including additional comparisons of mean LRRs.

617 **Appendix C.** Assessment of publication bias.

618 **Appendix D.** Assessment of data availability.

619 **Appendix E.** Additional results: Resampling and additional comparisons of mean LRRs.

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Table 1. List of species represented in the dataset by reef association, family common and scientific name, and species common and scientific names.

Reef Association	Family (common)	Common Name	Species
Resident	Toadfish (Batrachoididae)	Gulf toadfish	*Opsanus beta*
		Oyster toadfish	*Opsanus tau*
		Stiped blenny	*Chasmodes bosquianus*
		Florida blenny	*Chasmodes saburrae*
		Crested blenny	*Hypleurochilus geminatus*
		Feather blenny	*Hypsoblennius hentz*
		Freckled blenny	*Hypsoblennius ionthas*
		Highfin blenny	*Lupinoblennius nicholsi*
		Blenny species	*Blennidae* spp.
	Skilletfish (Gobiesocidae)	Skilletfish	*Gobiesox strumosus*
	Goby (Gobiidae)	Frillfin goby	*Bathygobius soporator*
		Darter goby	*Ctenogobius boleosoma*
		Freshwater goby	*Ctenogobius shufeldti*
		Emerald goby	*Ctenogobius smaragdus*
		Highfin goby	*Gobionellus oceanus*
		Naked goby	*Gobiosoma bosc*
		Seaboard goby	*Gobiosoma ginsburgi*
		Code goby	*Gobiosoma robustum*
		Clown goby	*Microgobius gulosus*
		Green goby	*Microgobius thalassinus*
		Goby species	*Gobiosoma* spp.; *Microgobius* spp.; Gobiidae
Transient	Grunt (Haemulidae)	Barred grunt	*Conodon nobilis*
		White grunt	*Haemulon plumierii*
		Pigfish	*Orthopristis chrysoptera*
	Snapper (Lutjanidae)	Gray snapper	*Lutjanus griseus*
		Lane snapper	*Lutjanus synagris*
	Swimming crab (Portunidae)	Blue crab	*Callinectes sapidus*
		Lesser blue crab	*Callinectes similis*

	Iridescent swimming crab	*Portunus gibbesii*
	Blotched swimming crab	*Portunus spinimanus*
	Swimming crab species	*Callinectes* spp.; Portunidae
Drum (Sciaenidae)	Silver perch	*Bairdiella chrysoura*
	Sand seatrout	*Cynoscion arenarius*
	Spotted seatrout	*Cynoscion nebulosus*
	Silver seatrout	*Cynoscion nothus*
	Weakfish	*Cynoscion regalis*
	Banded drum	*Larimus fasciatus*
	Spot croaker	*Leiostomus xanthurus*
	Southern kingfish	*Menticirrhus americanus*
	Northern kingfish	*Menticirrhus saxatilis*
	Atlantic croaker	*Micropogonias undulatus*
	Black drum	*Pogonias cromis*
	Red drum	*Sciaenops ocellatus*
	American stardrum	*Stellifer lanceolatus*
	Drum species	*Cynoscion* spp. Sciaenidae
Porgy (Sparidae)	Sheepshead	*Archosargus probatocephalus*
	Spottail seabream	*Diplodus holbrookii*
	Pinfish	*Lagodon rhomboides*

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Figure 1. Map of study sites along the Gulf of Mexico and Atlantic Coasts of the USA. States shaded in gray are represented in the dataset. Each point represents an independent study, with shapes representing tidal zone (circles represent intertidal reefs and triangles represent subtidal reefs). Additional study attributes are listed in Table A1.

Figure 2a-b. Mean and 95% confidence intervals of the Log Response Ratios (LRR) of nekton densities at oyster compared to unstructured sedimentary control habitats for each family (toadfish = Batrachoididae, blenny = Blenniidae, goby = Gobiidae, grunt = Haemulidae, snapper = Lutjanidae, crab = Portunidae, drum = Sciaenidae, porgy = Sparidae), at natural vs. restored reefs, for a) intertidal reefs, and b) subtidal reefs. Numbers indicate the total number of LRRs that contributed to the mean LRR for each family. Asterisks indicate 95% confidence intervals that do not overlap 0. NA indicates that data were insufficient to include in analyses, as there were fewer than 10 LRRs included in the mean.

Figure 3a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by reef size (m^2) on intertidal reefs. Point size is weighted by the number of independent replicates for each reef. The model for Toadfish (panel a) has a singular fit and should be interpreted with caution.

Figure 4a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by reef size (m^2) on subtidal reefs. Studies that included multiple experiments with reefs of different sizes are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. For readibility, mean LRRs (0.921 for toadfish, 0.679 for drums and 1.63

for porgies) for the study with the largest subtidal reef (> 8000 m^2; Table A1) are not pictured. The model for Gobies (panel c) has a singular fit and should be interpreted with caution.

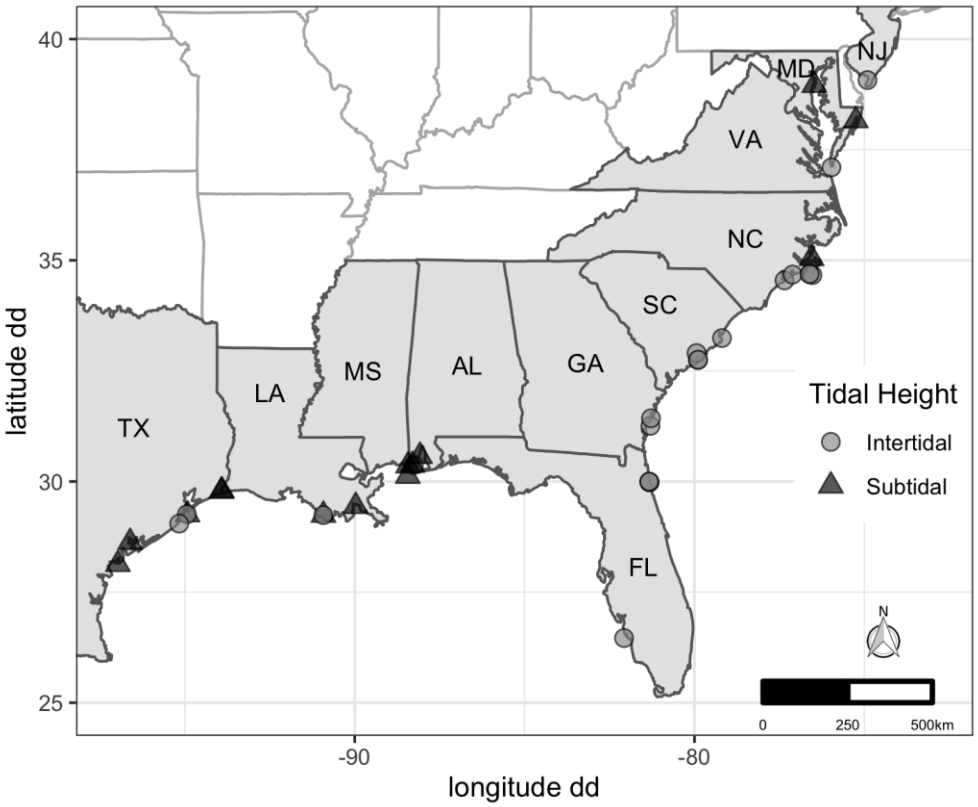
Figure 5a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by vertical relief (m) on intertidal reefs. Studies that included multiple experiments with reefs of different reliefs are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas) indicate a significant effect of vertical relief from single-family mixed model analysis. The model for Grunts (panel d) has a singular fit and should be interpreted with caution.

Figure 6a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by vertical relief (m) on subtidal reefs. Studies that included multiple experiments with reefs of different reliefs are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a solid trend line and 95% confidence intervals (gray areas) indicate a significant effect of reef age from single-family mixed model analysis. Dashed lines indicate vertical relief effects for which $0.05 \leq P \leq 0.1$.

Figure 7a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by reef age (years) on intertidal reefs. Studies that included multiple experiments with reefs of different ages are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a dashed trend line and 95% confidence intervals (gray areas) indicate a reef age from single-family mixed model analysis for which $0.05 \leq P \leq 0.1$. The model for Toadfish (panel a) has a singular fit and should be interpreted with caution.

Figure 8a-h. Variation in mean Log Response Ratios (LRR) of nekton densities by reef age (years) on subtidal reefs. Studies that included multiple experiments with reefs of different ages are assigned separate points for each reef. Point size is weighted by the number of independent replicates for each reef. Plots with a trend line and 95% confidence intervals (gray areas) indicate a significant effect of reef age from single-family mixed model analysis.

681 Figure 1.



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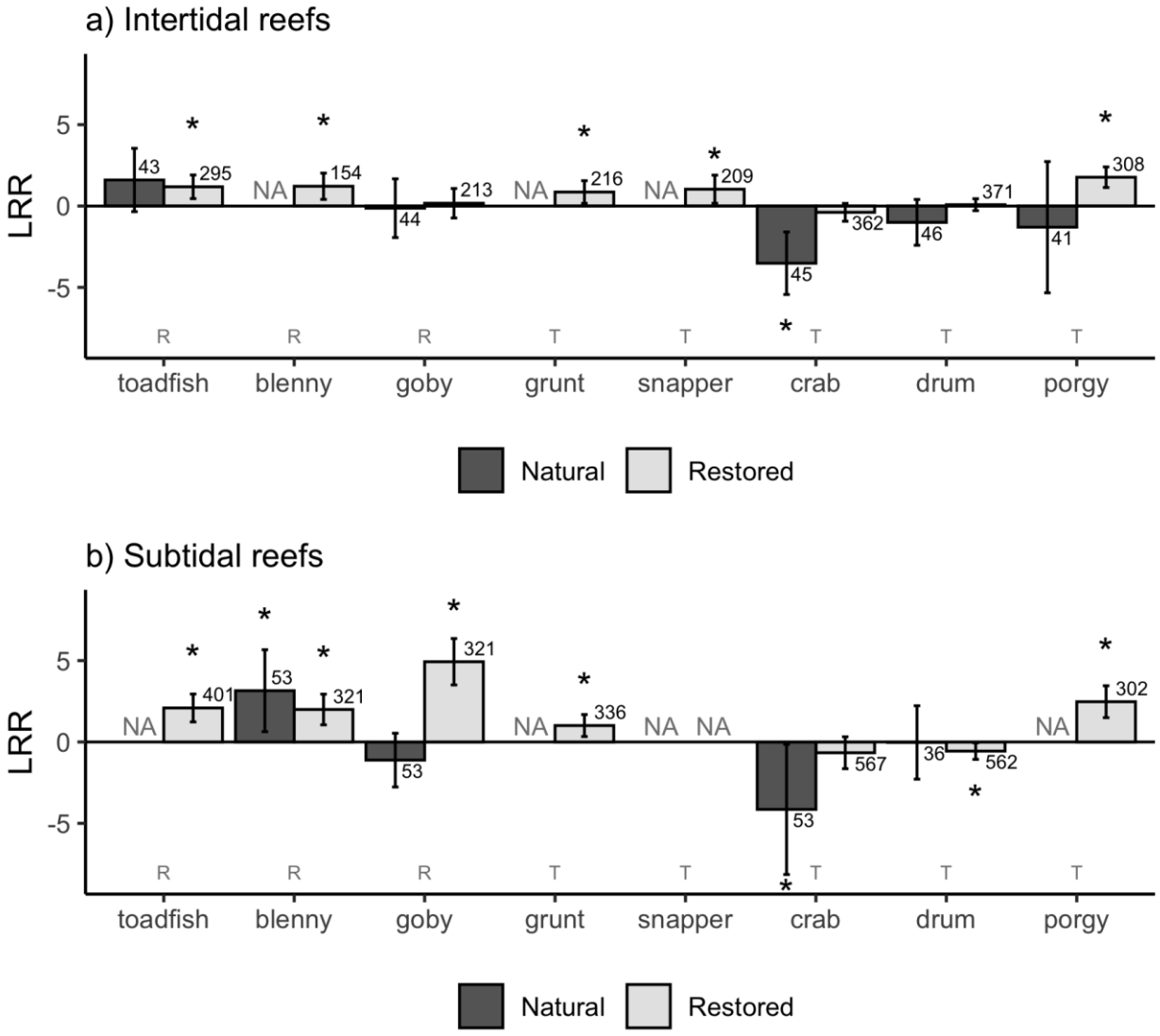
683 **Figure 2a-b.**



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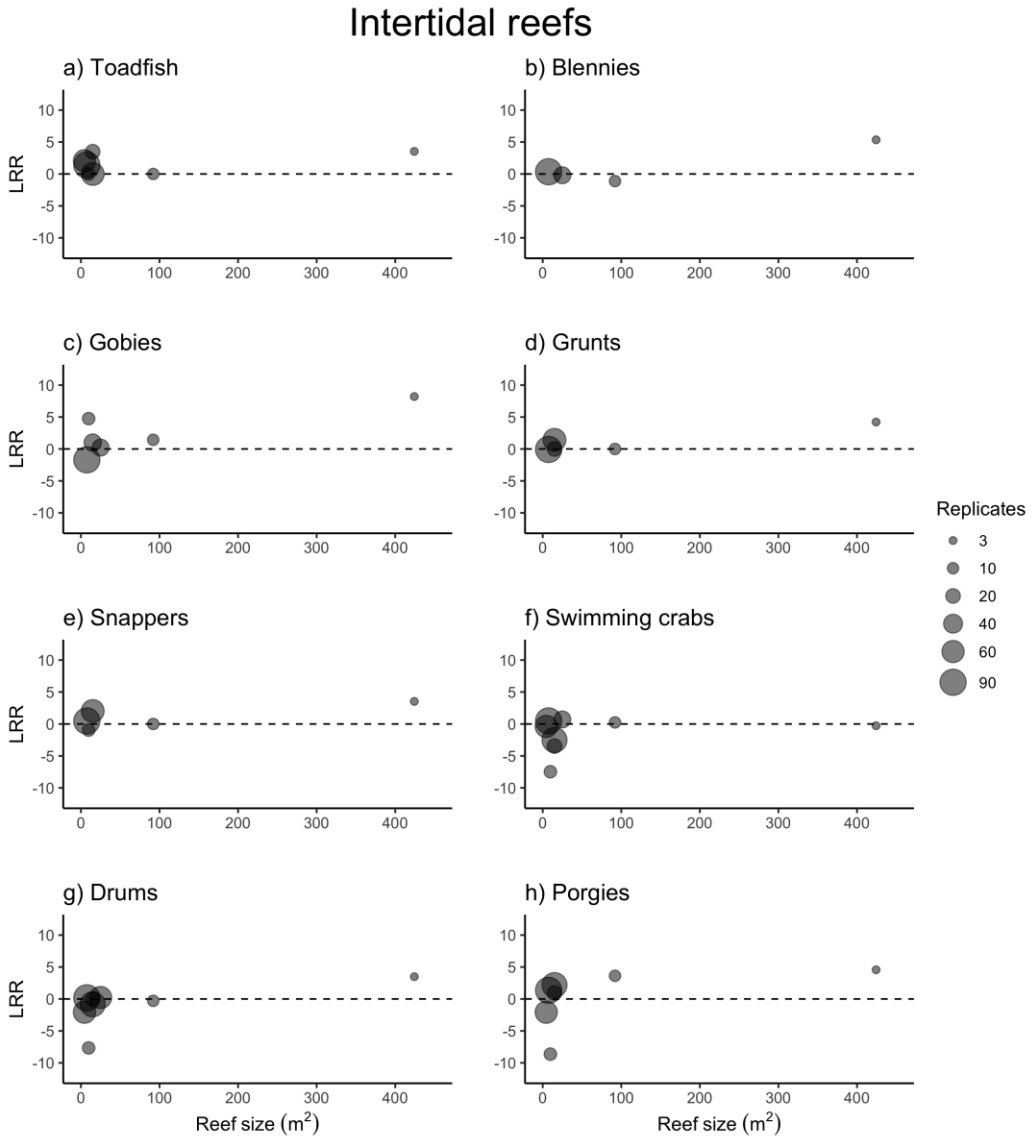
686 **Figure 3a-h.**



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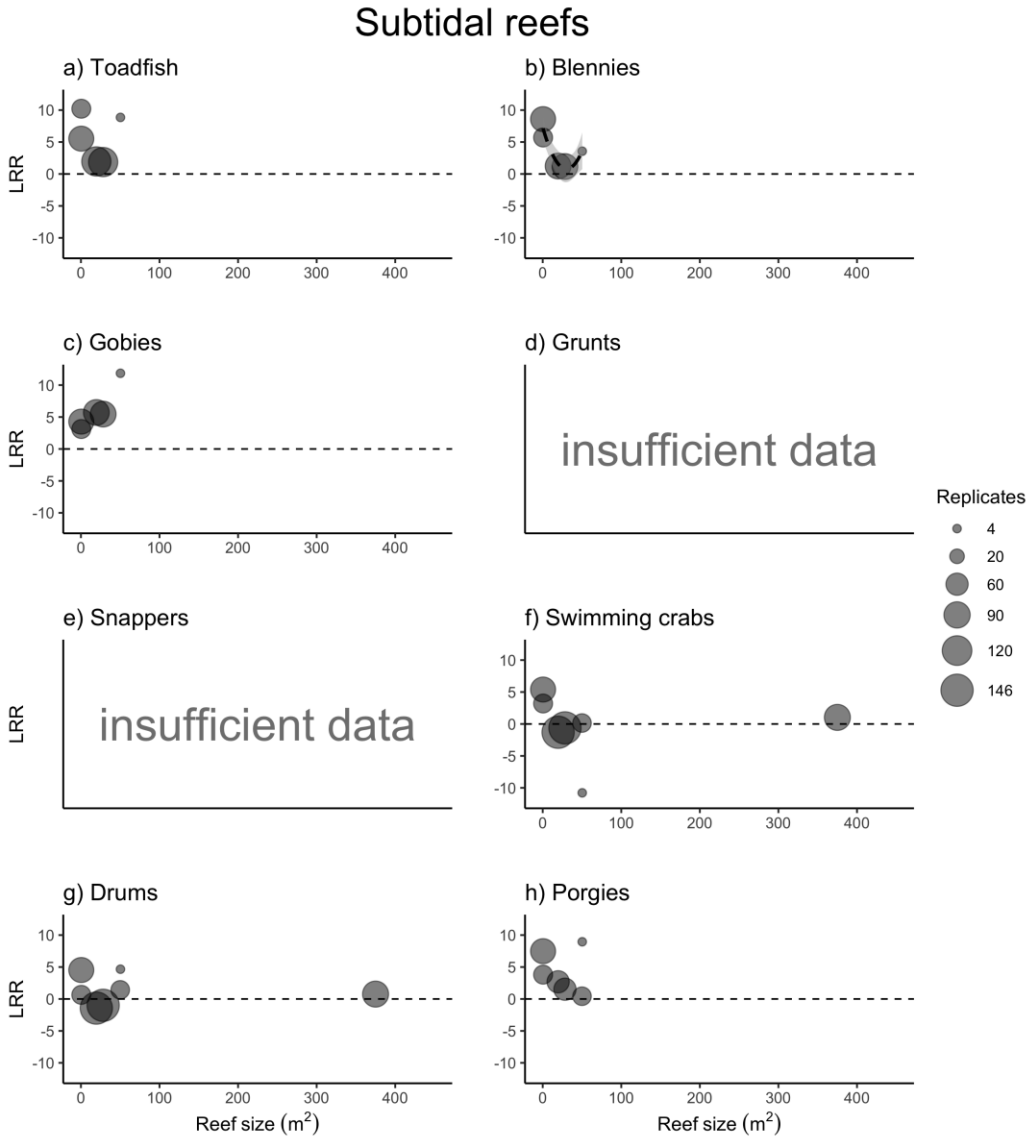
689 **Figure 4a-h.**



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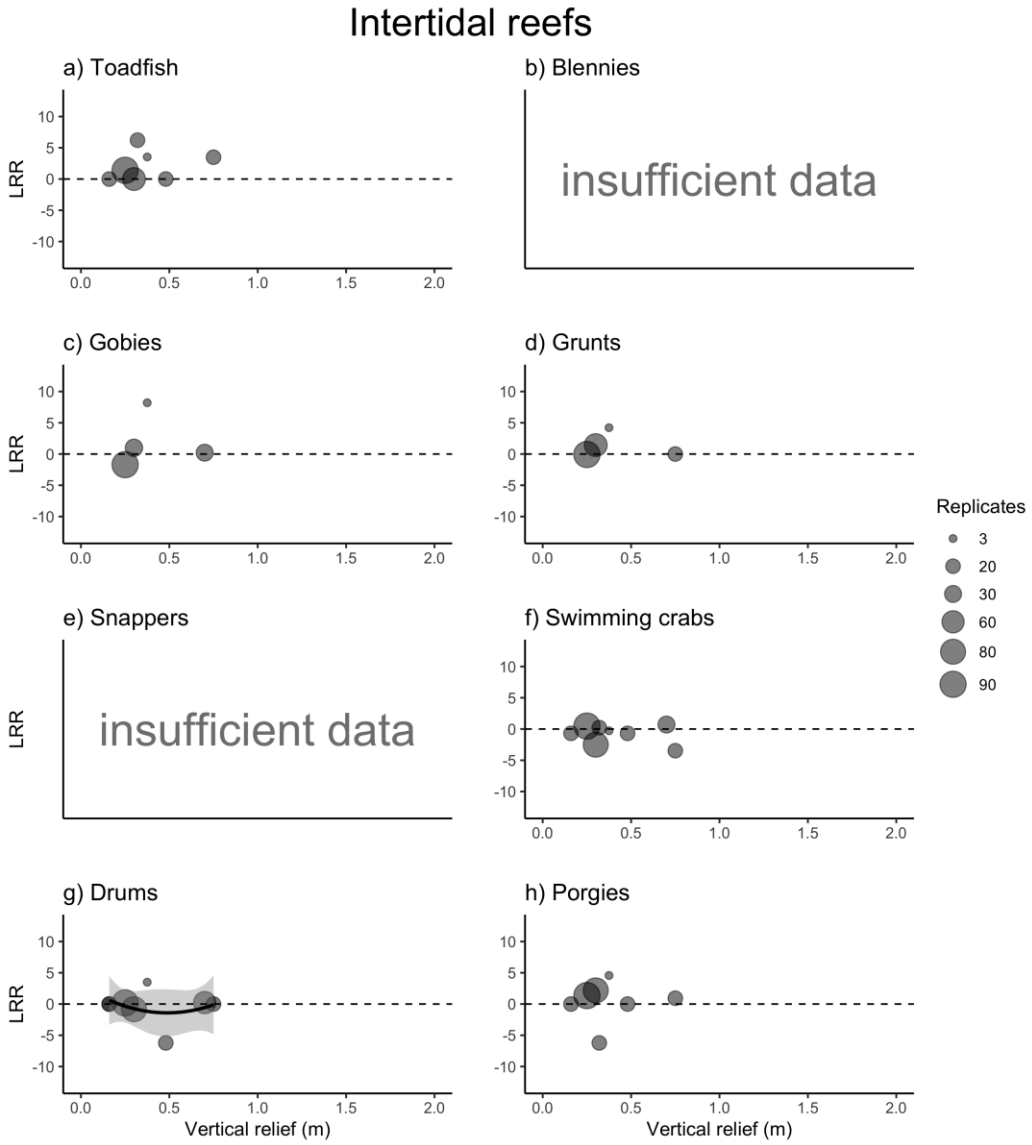
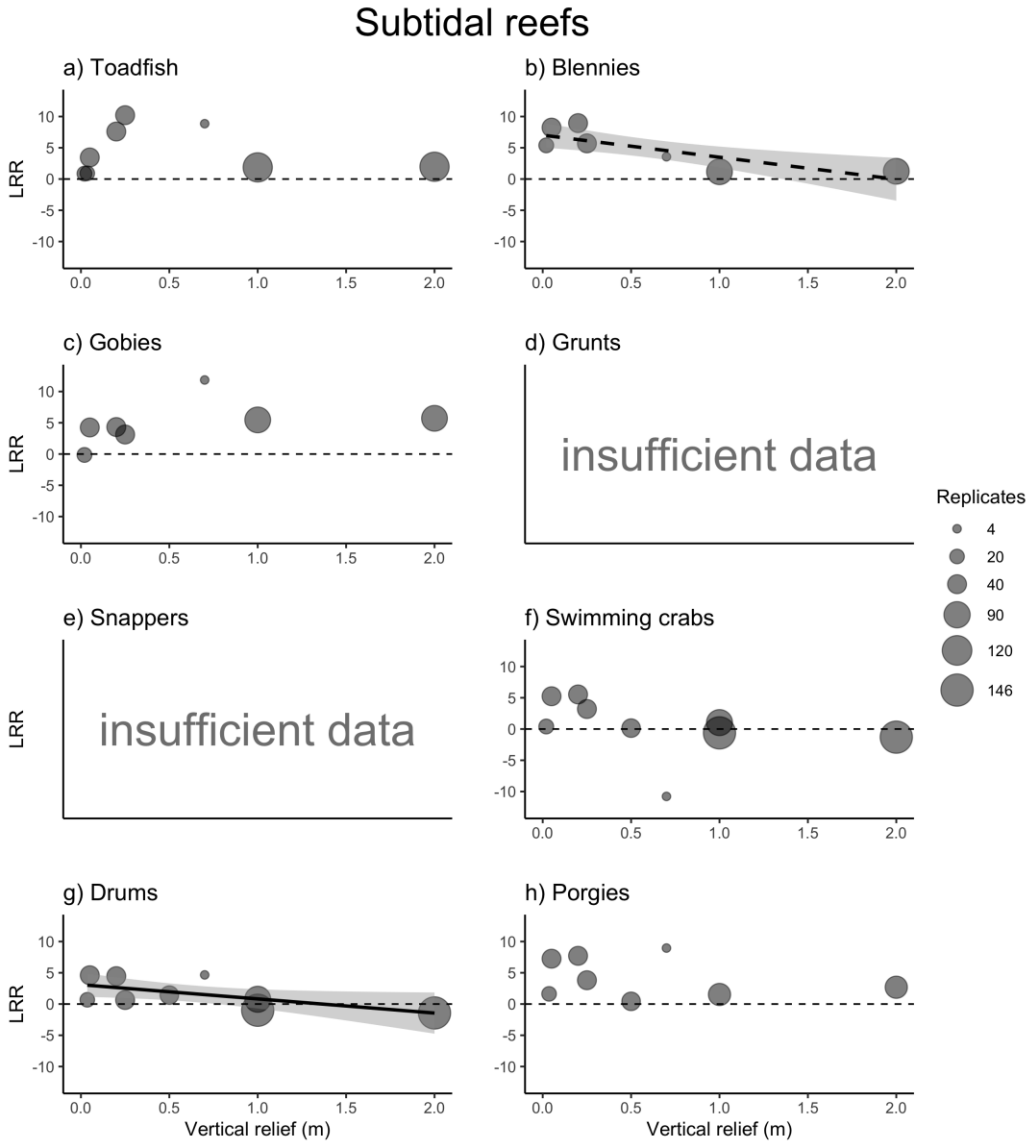
693 **Figure 5a-h.**

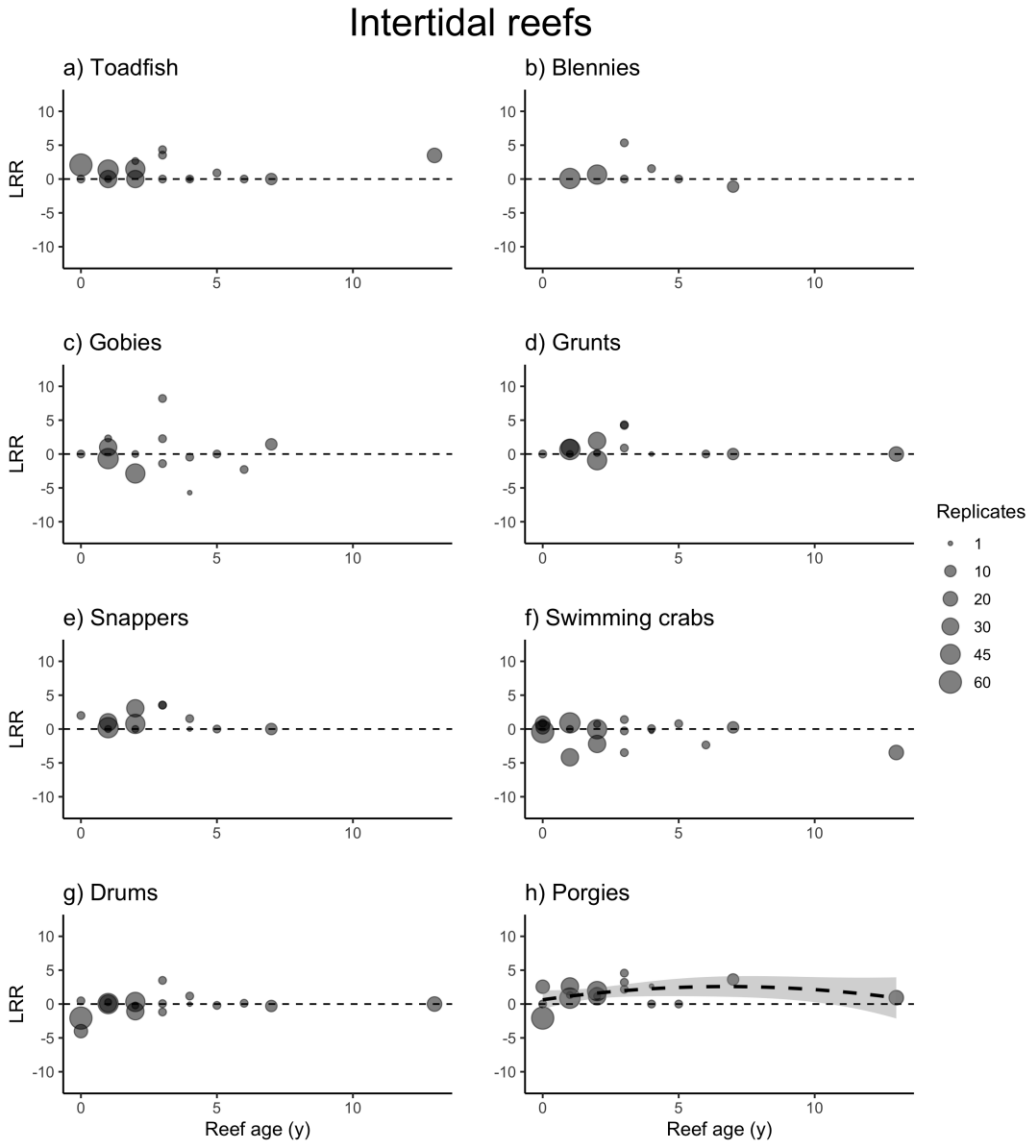


694

Figure 6a-h.


Subtidal reefs
a) Toadfish
b) Blennies
c) Gobies
d) Grunts
insufficient data
e) Snappers
insufficient data
f) Swimming crabs
g) Drums
h) Porgies
LRR
Vertical relief (m)
Replicates
4
20
40
90
120
146

698 **Figure 7a-h.**



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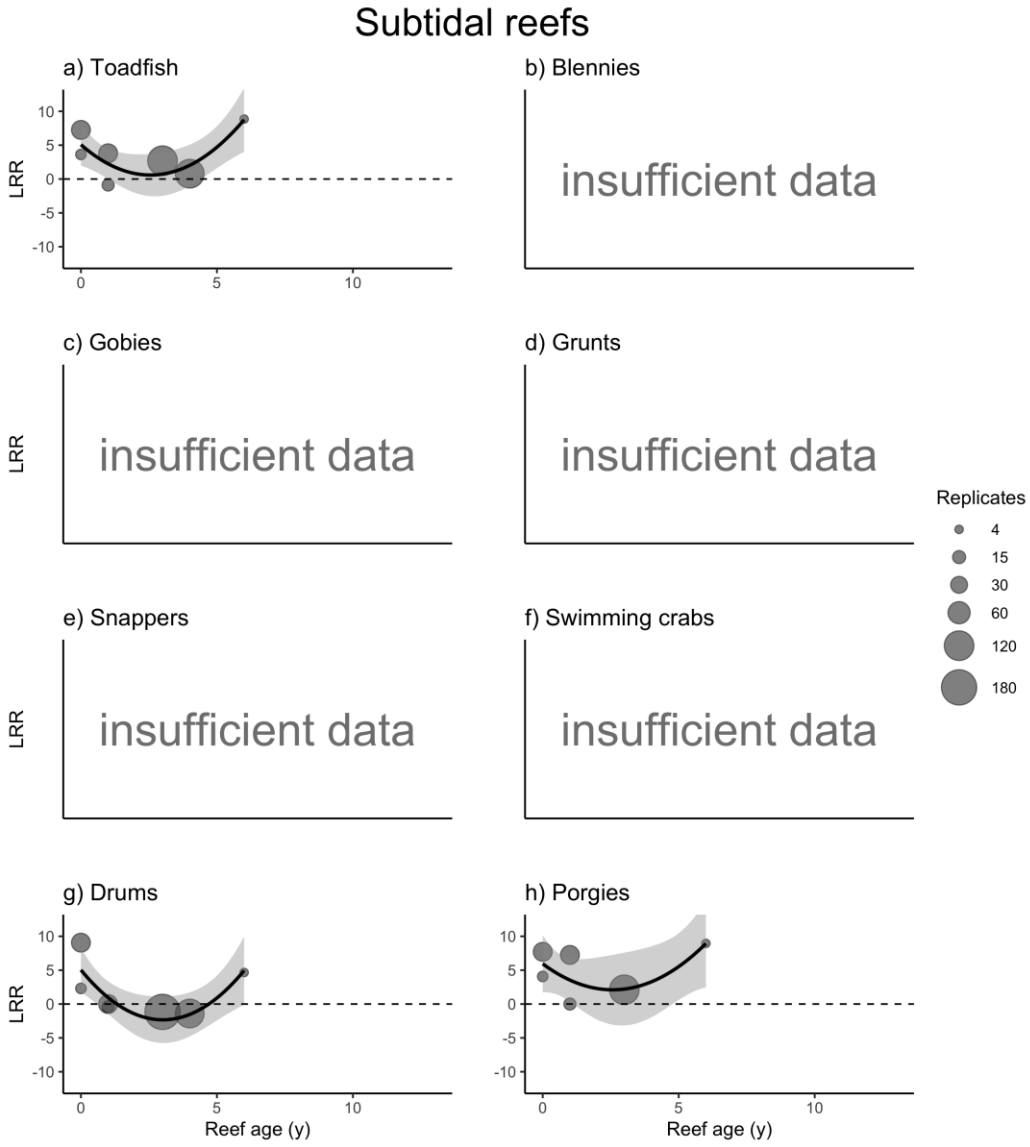
701 **Figure 8a-h.**



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